

POLYMORPHIC TERMINATION OF DIAPAUSE BY *CECROPIA*: GENETIC AND GEOGRAPHICAL ASPECTS

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The *Cecropia* moth, *Hyalophora cecropia* (L.) (Lepidoptera: Saturniidae), occurs over most of the United States and southern Canada east of the Rocky Mountains. It is apparently entirely univoltine, although Grote (1878) claimed that it is double-brooded in the south. The winter is spent as a diapausing pupa in a cocoon firmly attached to the food plant or a nearby shrub. The adults, which emerge in spring or early summer, do not feed and have an average life span of only about ten days (Rau and Rau, 1914). The larvae, which are polyphagous and feed on a variety of woody plant species, spin and pupate in late summer or early fall (Waldbauer and Sternburg, 1967; Scarbrough, 1970 and Ferguson, 1972).

Diapause in *Cecropia* has been thought to be obligatory (Williams, 1956), but Mansingh and Smallman (1966, 1967) reported that it can be prevented by exposing the larvae to a long photophase. They did not report the temperature at which the larvae were reared, unfortunate in view of the modifying effect of temperature on critical daylength which has been reported for other species (Danilevskii, 1965). Williams (1956) found that diapause could be terminated by prolonged exposure to low temperatures—for example, 10 weeks at 6° C. Mansingh and Smallman (1966, 1967) reported that diapause could also be terminated in unchilled pupae by long photophase, but thought that a long photophase had no effect on chilled pupae.

In an earlier paper (Sternburg and Waldbauer, 1969) we established that from 1966 to 1968 the emergence of adult *Cecropia* was bimodal under natural conditions in the vicinity of Urbana, Illinois. Data for three more years confirm our earlier findings and are presented below. Thus, from 1966 to 1971 from 4.7% to 15.6% of the adults emerged from over-wintering pupae during late May and the first few days of June (Group I) while the remainder emerged during the second half of June and the first few days of July (Group II). It seems safe to conclude that the emergence of adult *Cecropia* is consistently bimodal—at least in the vicinity of Urbana.

We do not know how widely it occurs over the range of the species, but the bimodal emergence of *Cecropia* is clearly not just a local phenomenon. Data presented by Marsh (1941) indicate a bimodal emergence in Chicago, Illinois in 1933. Dr. A. M. Young (Department of Biology, Lawrence University, personal communication) found the emergence to be bimodal in Chicago in 1968, and we (see below) found it to be bimodal there in 1970. Rau and Rau (1912, 1914) presented data which show clearly that the emergence of *Cecropia* was bimodal in St. Louis, Missouri in 1910, 1911 and 1913. Data from other parts of the range would be of great interest but are not available.

A comparable bimodality has not been demonstrated by investigators who worked extensively with *Cecropia* under laboratory conditions (Williams, 1956; Mansingh and Smallman, 1966 and 1967). The reason is unknown. Perhaps they

used populations which are not polymorphic for diapause termination—if such populations exist—or perhaps the polymorphism was not expressed under the conditions they used in the laboratory. Williams (1956, Fig. 3) did report a bimodal emergence which extended over a twenty-four week period and was obviously the result of insufficient chilling. We have made similar observations. If wild local pupae are brought into the laboratory at the beginning of December some adults emerge from them two to three months later while most of the remaining surviving adults emerge nine to twelve months later. This appears to be a different phenomenon than the bimodal emergence which under natural conditions extends over a period of only about eight weeks. Williams (1956, Table III) noted two instances of bimodality which might be comparable to our observations, but whether or not they actually are comparable cannot be determined because he presented only the data derived from the primary mode.

Bimodality is not brought about just by an intrinsic difference in the rates at which adult development proceeds in the two groups. Observations made at regular intervals in an outdoor insectary at Urbana in 1968 showed that the median date on which development was initiated (as signalled by the retraction of the epidermis in the area of the legs) was April 1 for Group I but June 3 for Group II. The median emergence dates were May 31 for Group I and June 26 for Group II (Willis, Waldbauer and Sternburg, 1974). Thus, Group II began to develop 63 days later than Group I although the interval between the median emergence dates was only 26 days. The discrepancy is due to the fact that Group I initiated development while the weather was still cool and, therefore, required a mean of about 59 days to complete development, while Group II, which initiated development when the weather was much warmer, required a mean of only about 25 days to complete development.

The extent to which one may validly extrapolate what happens under natural conditions from the results of the published laboratory studies of diapause termination in *Cecropia* is by no means obvious. Nevertheless, the results obtained by Williams (1956) have often led to the supposition that under natural conditions winter chilling breaks diapause in all pupae, and that all pupae begin to develop as soon as it becomes warm enough, synchronization of individuals with each other occurring because all develop at more or less the same temperature and, therefore, at more or less the same rate. Something like this does seem to be true of Group I, but it is definitely not true of Group II. Group II pupae are capable of deferring the initiation of development for over two months under conditions which permit the initiation and completion of development in Group I pupae. Obviously there are unexpected complexities involved in the resumption of development by *Cecropia* pupae, and, as will be discussed below, these complexities permit a precise and subtle adjustment to climatic and ecological conditions.

We have not made an exhaustive search of the literature for cases of polymorphic termination, but a careful scrutiny of several of the more recent reviews (deWilde, 1962; Danilevskii, 1965; Beck, 1968; Danilevskii, Goryshin and Tyschenko, 1970) suggests that the polymorphic termination of diapause is either an infrequent phenomenon or that it tends to go unrecognized. Danilevskii (1965, page 203) cites a report that the emergence of the cotton bollworm (*Chloridea obsoleta*) from overwintering pupae is bimodal in the Caucasus. The emergence of tobacco hornworms (*Manduca sexta*) from overwintering pupae is bimodal in North Carolina

(Rabb, 1966). It has long been known that the emergence of the zebra swallowtail (*Eurytides marcellus*) from overwintering pupae is bimodal, and that in this case the dimorphism involves color and form as well as physiology (Scudder, 1889, pages 1273-1278).

We have used the phrases "resumption of development" and "termination of diapause" as if they are interchangeable. This is the common usage and is consistent with the terminology proposed by Mansingh (1971). However, it should be recognized that this usage tends to obscure the complexity of diapause termination. For example, Mansingh (1971) recognized that insects which are "in diapause" may be in either the "refractory phase" or the "activated phase." Thus, insects which have received insufficient chilling are not competent to resume development, and would be considered refractory, while insects which have received sufficient chilling begin to develop soon after they are warmed up and would be considered activated.

MATERIALS AND METHODS

Collecting cocoons

The cocoons which will henceforth be referred to simply as the "Urbana cocoons" were collected by the authors from the native wild population in the vicinity of Urbana, Illinois (approximately 40°6' north latitude). Approximately 95% were collected from trees and shrubs in the twin cities of Champaign and Urbana; the remainder were taken in similar situations in the surrounding countryside or nearby small towns. Further details were given by Waldbauer and Sternburg (1967) and by Sternburg and Waldbauer (1969).

In 1967 wild cocoons were collected by Dr. Allen M. Young in Chicago, about 120 miles to the north of Urbana. About one-third were taken from willows along the Illinois Central Railroad tracks about one mile south of the intersection of Michigan and Madison Avenues (approximately 41°51' north latitude); about one-half were taken along the same tracks about ten miles to the south; the remainder came from various localities within the Chicago city limits. These cocoons were moved to Urbana on December 19, 1967. On December 15, 1969 the authors, Dr. Aubrey Scarbrough and Dr. Young made another collection of cocoons from the sites along the railroad tracks mentioned above. The cocoons were taken to Urbana that day, but the next day one-half of them plus a number of cocoons collected in Urbana were transferred to the Morton Arboretum at Lisle, Illinois (approximately 41°47' north latitude) about twenty-five miles west of the intersection of Michigan and Madison.

Rearing

Females were mated either by placing them in a cage with a male or by placing them outdoors in a flight trap (Sternburg and Waldbauer, 1969) where they mated with a wild male. The latter technique was used when Group I males were on the wing, and only in the selection of early emerging strains from the local population. Inseminated females, confined in large brown paper bags in the laboratory, fastened about 300 eggs to the sides of the bag in five or six days. When the eggs were nearly ready to hatch the bags were ripped open and placed

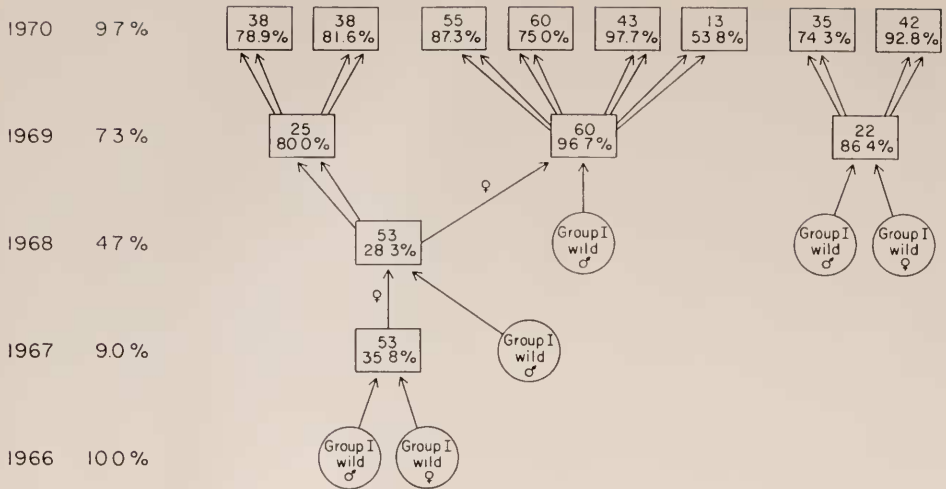


FIGURE 1. The descent of the eight groups of *Cecropia* siblings, line selected from the Urbana population for emergence with Group I, which emerged as adults in 1970. On the left are the year of emergence and the percentage of the wild population which emerged with Group I in each year. A circle indicates a wild parent, a box the progeny resulting from a controlled mating. The upper figure in each box shows total progeny reared; the lower shows the percentage which emerged with Group I. Arrows show parentage; sex is indicated only where necessary.

under large nylon mesh sleeves (Telfer, 1967) which covered entire apple trees (*Malus pumila*) and were securely tied shut at the base of the trunk. The trees were usually almost defoliated by the time the larvae became third instars; the larvae were then moved to fresh trees—about thirty to a net—where they usually managed to complete their growth without running short of food. In late summer or early fall the nets were removed and the cocoons were harvested.

Maintenance of pupae

Cocoons were kept in screened cages in a screened outdoor insectary at either Urbana or the Morton Arboretum, and were exposed only to natural photoperiods and temperatures. From late April to mid-July the cages were examined daily for newly emerged adults. The date of emergence and sex were noted except at the Morton Arboretum where sex was not noted. Reared animals were indoors only when mating and/or ovipositing. Wild or reared cocoons were sometimes brought into the laboratory for a few hours for counting and sorting.

The daily mean temperatures indicated on Figures 2-4 for Urbana were provided by the Illinois State Water Survey. Daily means for the Morton Arboretum (Fig. 3) were calculated from daily maximum and minimum temperatures provided by the Environmental Data Service of the U. S. Department of Commerce.

Selection of early-emerging strains

Beginning in 1966 we made line selections for early emergence (Group I) from the population native to the Urbana area. In every instance the group affiliation of

individuals was determined by reference to the seasonal pattern of emergence from a group of locally collected wild pupae held for the winter in the same insectary. From 1966 to 1968 the emergence pattern was further confirmed by using traps baited with virgin females to catch males from the remaining local wild population (Sternburg and Waldbauer, 1969). We made frequent outcrosses because inbreeding led to a disastrous reduction in viability. Five females which were the F_1 progeny of a wild pair and had been mated with their sibs laid a mean of 238 eggs, but only 54.4% of them hatched. Three females, including two from the same group of siblings, mated with wild males laid a mean of 297 eggs, 96.8% of which hatched. Figure 1 shows the pedigrees of all of the groups selected for emergence with Group I which emerged in 1970. All of our line selections were similarly made. We made several matings of Group II adults, but did not make a serious effort to select for emergence with Group II. It might be possible to mate Group I adults with Group II adults if the lives of Group I adults could be prolonged by holding them in a refrigerator. However, we did not attempt this. Mating and rearing were handled as described above. It was usually not possible to rear all of the progeny resulting from a mating. Therefore, when most of the larvae in a group were third instars we discarded the excess, retaining a group approximately typical of the whole with respect to distribution by instar and size.

RESULTS

Selection for emergence with Group I

Table I summarizes the results of all of the controlled matings which we made from 1966 to 1970. An examination of either this table or of Figure 1 leaves no doubt that the bimodal emergence of adult cecropia has a genetic basis. In three years or less we were able to select from the local population strains which averaged over 75% emergence with Group I as compared with the average of about 8% which was typical of the local wild population (Table II).

We made several controlled matings of wild Group II moths in 1966 (Table I), but made no real effort to select for emergence with this group. Our only attempts in this direction (Table I, 1968) led to an apparent decrease in the proportion of adults which emerged with Group II. However, the number of moths involved is small and this result may not be typical.

Even after several years of selection both Groups I and II remained essentially in phase with the corresponding groups of the wild population as indicated by the median emergence dates in Table I. Median dates do not, of course, tell the whole story. However, a closer comparison shows that with either Group I or II the individual emergence dates of the progeny of the various controlled matings listed in Table I generally fell within the range of dates over which the corresponding wild adults emerged. In only 10 out of 32 cases did a few individuals emerge before or after the corresponding group of the wild population, and then the discrepancy was only from one to four days. There was clearly no tendency to produce intermediates. In fact, our data suggest the opposite tendency. From 1967 to 1971 the number of days from the emergence of the last individual of Group I to the emergence of the first individual of Group II of the wild population ranged from 6 to 16 and averaged 10.4. On the other hand, the corresponding figures for

TABLE I

Yearly distribution between the two emergence groups of adult *Cecropia* line selected from the Urbana population for emergence with either Group I or Group II. The distribution of adults emerging each year from field-collected pupae is given for comparison. "Wild" refers to members of the local wild population which emerged with the indicated group either in the field or in the insectary from pupae collected in the field. "Selection" refers to the F_1 or F_2 progeny resulting from controlled matings

Year of emergence	Type of mating	Total no.		Emerging with Group I			Emerging with Group II		
		Matings	Moths	Mean %	Range in %	Median emergence date	Mean %	Range in %	Median emergence date
1967	(Field collected)*	—	167	9.0	—	May 26	91.0	—	June 20
	Gp I wild × Gp I wild	4	119	23.5	0-35.8	May 26	76.5	64.2-100	June 18
	Gp II wild × Gp II wild	5	78	5.1	0-9.7	May 24	94.9	90.3-100	June 17
1968	(Field collected)*	—	557	4.7	—	May 24	95.3	—	June 20
	Gp I wild × Gp I wild	2	111	4.5	4.2-4.7	May 21	95.5	95.3-95.8	June 20
	Gp I selection × Gp I wild	2	87	21.8	11.8-28.3	May 26	78.2	71.7-88.2	June 22
	Gp I selection × Gp I selection	2	29	17.2	14.3-20.0	May 22	82.8	80.0-85.7	June 23
	Gp II selection × Gp II selection	2	47	14.9	6.7-18.8	May 30	85.1	81.2-93.3	June 19
1969	(Field collected)	—	409	7.3	—	May 24	92.7	—	June 24
	Gp I wild × Gp I wild	1	22	86.4	—	May 25	13.6	—	June 17
	Gp I selection × Gp I wild	3	103	89.3	72.7-96.7	May 25	10.7	3.3-27.3	June 17
	Gp I selection × Gp I selection	2	34	64.7	22.2-80.0	May 24	35.3	20.0-77.8	June 26
1970	(Field collected)	—	165	9.7	—	May 19	90.3	—	June 15
	Gp I selection × Gp I selection	8	324	82.7	53.8-97.7	May 14	17.3	2.3-46.2	June 13
1971	(Field collected)	—	270	15.6	—	May 21	84.4	—	June 17
	Gp I selection × Gp I selection	8	98	72.4	23.1-100	May 23	27.6	0-76.9	June 17

* Data from Sternburg and Waldbauer (1969).

TABLE II

Summary of distribution between the two emergence groups of *Cecropia* adults from wild pupae collected in Urbana or pupae which resulted from controlled matings of Urbana moths, 1967-1971

	No. matings	Emerging with GP I		Emerging with GP II	
		No.	%	No.	%
Field collected (1967-1971)	—	129	8.2	1,439	91.8
Gp I wild × Gp I wild (1967-1969)	7	52	20.6	200	79.4
Gp I selection × Gp I wild (1968-1969)	5	111	58.4	79	41.6
Gp I selection × Gp I selection (1968-1971)	20	366	75.5	119	24.5
Gp II wild × Gp II wild (1967)	5	4	5.1	74	94.9
Gp II selection × Gp II selection (1968)	2	7	14.9	40	85.1

all Group I controlled matings lumped by year from 1967 to 1971 are 7 to 26 days with a mean of 14.4 days. This wider spacing between the two groups is due largely to a tendency for the emergence of Group I progeny of controlled matings to cluster more tightly about the median. Selection for emergence with Group I did not, however, lead to a greater spread between the median emergence dates of Groups I and II. In the wild population the number of days between the median emergence dates of Groups I and II ranged from 25 to 31 and averaged 27.4. For all progeny of Group I controlled matings lumped by year the corresponding figures are 23 to 33 days with a mean of 27.3 days.

Sternburg and Waldbauer (1969) reported that in each group the males emerge earlier than the females, and that Groups I and II are distinguished not only by an interval of no emergence, but also by the alternating emergence of males and females. This held true for the progeny of controlled matings reported on in this paper. We also reported that Group I is characterized by a sex ratio which favors

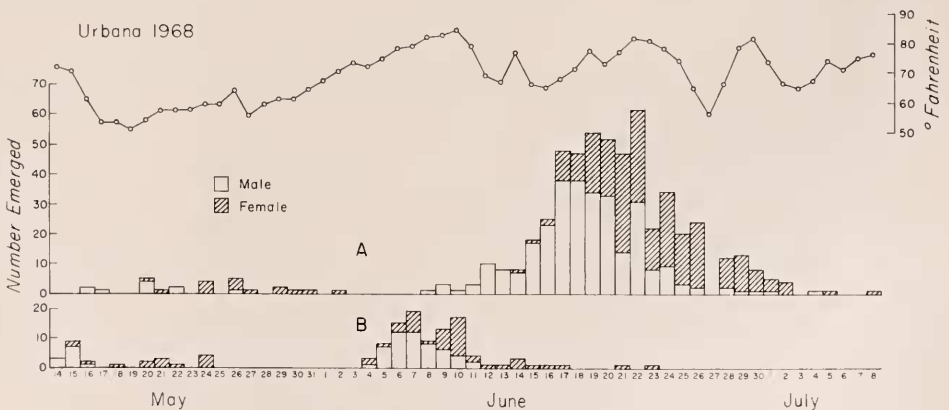


FIGURE 2. Emergence of adult *Cecropia* at Urbana, Illinois in 1968 from wild cocoons collected in the field and moved into a screened outdoor insectary by late fall; (A) cocoons collected in the vicinity of Urbana; (B) cocoons collected in Chicago. The daily mean temperatures are plotted above the histograms.

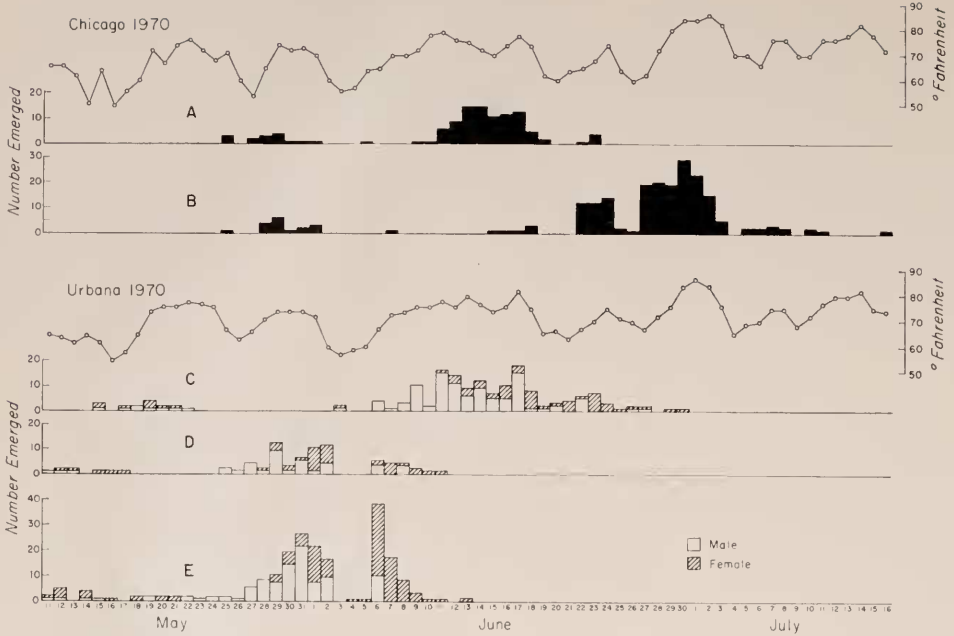


FIGURE 3. Emergence of adult *Cecropia* in 1970 from cocoons moved into a screened outdoor insectary at either the Morton Arboretum near Chicago (A and B) or at Urbana (C, D and E) by late fall. The origin of the cocoons is as follows: (A) wild, collected in Chicago, (B and C) wild, collected in Urbana, (D) wild, collected in Chicago, and (E) F_2 progeny reared in Urbana from wild parents collected in Chicago in 1967-68. The daily mean temperatures are plotted above the histograms.

females, and Group II by a ratio which favors males. This held only partially true for the progeny of Group I controlled matings. In 1967 and 1968 those which emerged with Group I were consistently mostly females (75% overall), but from 1969 to 1971 the sex ratio consistently approximated 50-50 (overall 48.8% females). On the other hand, the Group II progeny of Group I controlled matings were consistently mostly males (overall 60.9%) from 1967 to 1970 although in 1971 there were only 44.4% males.

Wild adults of both Groups I and II produced some progeny which emerged with Group I and others which emerged with Group II (Tables I and II). A majority of the progeny produced by either group emerged with Group II, but Group I adults usually produced a greater proportion of Group I progeny. Seven matings of wild Group I moths made from 1966 to 1968 produced an average of 20.6% Group I progeny while in the same years an average of only 7.0% of the wild population emerged with Group I. On the other hand, five matings of wild Group II moths made in 1966 produced only 5.1% Group I progeny as compared with the 9% produced by the wild population in the same year.

Latitudinal adaptations in diapause termination

Wild *Cecropia* collected as pupae in Chicago in the autumns of 1967 and 1969, and transferred to the outdoor insectary at Urbana were partially out of phase

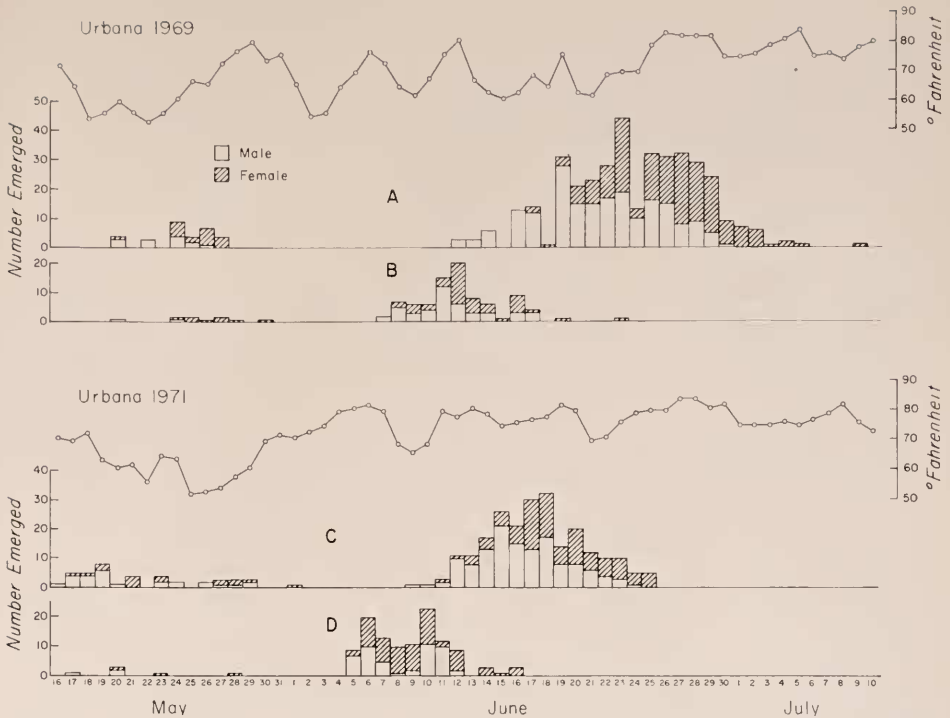


FIGURE 4. Emergence of adult cecropia in 1969 and 1971 from cocoons moved into a screened outdoor insectary at Urbana by late fall. The origin of the cocoons is as follows: (A) wild, collected in Urbana, (B) F_1 progeny reared in Urbana from wild parents collected in Chicago in 1967-68, (C) wild, collected in Urbana, and (D) F_1 progeny reared in Urbana from wild parents collected in Chicago in 1969-70. Mean daily temperatures are plotted above the histograms.

with the local population when the adults emerged the following spring. The reciprocal transfer made in the fall of 1969 revealed that Urbana moths were also partially out of phase with the local population after transfer to the Chicago area early in the pupal stage. In either case the transferred Group I moths were more or less in phase, while the transferred Group II moths were strikingly out of phase with the corresponding groups of the local population (Figs. 2 and 3).

Rearing *Cecropia* from the Chicago population in Urbana demonstrated that the difference in emergence time between the two populations has a genetic basis. The Group II descendants of Chicago *Cecropia* remained out of phase with the local Group II population for two generations in one instance (Fig. 3, E) and one generation in two instances (Fig. 4, B and D). Furthermore, after two generations in Urbana the descendants of Chicago *Cecropia* still emerged in phase with the adults from wild pupae which had been transferred from Chicago to Urbana the previous autumn (Fig. 3, D and E). We did not rear Urbana *Cecropia* in Chicago.

As pointed out above, Group I *Cecropia* transferred from Chicago to Urbana or *vice versa* continued to emerge more or less in phase with the local populations

TABLE III

Emergence of adult Cecropia from local cocoons and from cocoons transported between Chicago and Urbana. Unless otherwise indicated cocoons were collected from the wild population in the area of origin and transported no later than December 19. F₁ and F₂ indicate the first and second filial generations reared in Urbana from wild parents collected in Chicago

Origin and ultimate location of pupae	No. adults emerging	% emerging with Gp I	Median emergence date:	
			GP I	GP II
1968				
Urbana in Urbana*	557	4.7	May 24	June 20
Chicago in Urbana	119	17.6	May 16	June 8
1969				
Urbana in Urbana	409	7.3	May 24	June 24
Chicago in Urbana (F ₁)	97	11.3	May 25	June 12
1970				
Urbana in Urbana	165	9.7	May 19	June 15
Chicago in Urbana	72	11.1	May 13	June 1
Chicago in Urbana (F ₂)	220	9.5	May 14	June 1
Chicago in Chicago	111	14.4	May 29	June 15
Urbana in Chicago	208	8.6	May 29	June 29
1971				
Urbana in Urbana	270	15.6	May 21	June 17
Chicago in Urbana (F ₁)	120	5.0	May 20	June 9

* Data from Sternburg and Waldbauer (1969).

(Figs. 2-4). A few of these emergence curves suggest a tendency for Chicago Group I *Cecropia* in Urbana to emerge slightly earlier than local moths, and the median emergence dates listed in Table III to differ in some cases. However, reference to the curves (Fig. 2, Fig. 3, C and D, C and E) shows that whenever the dates differ the emergence of the two groups nevertheless overlaps to a large extent.

On the other hand, Group II *Cecropia* transferred either from Chicago to Urbana or *vice versa* were invariably widely out of phase with the local population. Chicago moths reared in Urbana or transferred as pupae emerged from 8 to 14 days *earlier* than the local population (Figs. 2 to 4). Conversely, the Group II Urbana moths in Chicago emerged 14 days *later* than the local population (Fig. 3, A and B).

It should be noted that in any case—whether a transfer is involved or not—the emergence of Group II follows sooner after the emergence of Group I in the Chicago population than it does in the Urbana population. The time which elapses from the median emergence date of Group I to the median emergence date of Group II varies somewhat from year to year, but remains more or less constant for each population, averaging 19 days for the Chicago population and 28 days for the Urbana population. The difference was invariably greater in the Urbana population (Table IV). It is, of course, adaptive for the difference in emergence time between the two groups to decrease to the north since less delay is possible where the season is shorter.

The reciprocal transfers of 1969-70 showed that, with respect to the population left behind, being moved to the north delays the emergence of both Groups I and

II while being moved to the south accelerates the emergence of both Groups I and II (Fig. 3, A to D, Table III). This is, of course, the expected result. From Urbana pupae in Chicago, Group I and II moths emerged respectively 10 and 14 days *later* than their counterparts in Urbana. From Chicago pupae in Urbana, Group I and II moths emerged respectively 16 and 14 days *earlier* than their counterparts in Chicago.

DISCUSSION

The polymorphic termination of diapause by *Cecropia*, considered either from the ecological or the physiological point of view, appears to be of considerable importance to the species. The difference in the emergence times of the two groups, consistently almost a month in the Urbana area, is equal to at least one-fifth of the growing season available to *Cecropia* at this latitude. It is almost inconceivable that such a large difference does not have profound ecological implications for the species. From a physiological point of view, the consistent difference of over two months in the onset of development by the two groups cannot be considered to be trivial.

We believe that *Cecropia*'s dimorphic termination of diapause is adaptive. The strategy involved is perhaps best expressed by the metaphor which warns against putting all of the eggs in one basket. *Cecropia*'s dimorphism avoids the placing of all of the progeny of a pair in one "temporal basket" in the following growing season at the critical period encompassing adult development, emergence and reproduction. Partitioning the progeny between an early and a late emergence group might allow at least some of the progeny of a pair to escape various detrimental factors which may occur at different times in the growing season, but do not occur in every year or vary in severity from year to year, such as some variations of the

TABLE IV

Days between median emergence dates of adult Cecropia from local cocoons and cocoons transferred between Chicago and Urbana. See Table III for further information

Origin, ultimate location of pupae and year	Days
Chicago in Chicago—1970	17
Chicago in Urbana—1968	23
Chicago in Urbana—1970	19
Chicago (F ₁) in Urbana—1969	18
Chicago (F ₁) in Urbana—1970	20
Chicago (F ₂) in Urbana—1970	18
Mean	19.2
Urbana in Urbana—1966	26
Urbana in Urbana—1967	26
Urbana in Urbana—1968	27
Urbana in Urbana—1969	31
Urbana in Urbana—1970	27
Urbana in Urbana—1971	27
Urbana in Chicago—1970	31
Mean	27.9

weather. Such detrimental factors might affect the developing pharate adults, the emerged adults or their progeny. For example, Group II and their progeny might escape the effects of unseasonably cold weather early in the season which might be disastrous for Group I, killing either the Group I adults themselves or their progeny. On the other hand, in another year the progeny of Group I moths might complete their larval development early enough to avoid a late summer drought which might be disastrous for the progeny of Group II. This strategy could also be selected for by other factors; for example, pressure from a parasitoid whose population fluctuates greatly from year to year and which attacks the progeny of only one of the emergence groups. The strategy of dimorphic diapause termination still allows exploitation of the entire growing season in a year in which the detrimental factors do not occur. The relevant factors may be difficult to identify if they are of relatively infrequent occurrence.

The proportion of individuals which emerge with the two groups varies from year to year. In Urbana from 1967 to 1971 Group I varied from 4.7% to 15.6% of the total (Table I). In St. Louis, Missouri Group I varied between 18% and 58% of the total from 1910 to 1913 (Rau and Rau, 1912 and 1914). The large differences in St. Louis suggest differential mortality, and are probably evidence of major shifts in the balance of factors which determine the relative survival of members of the two emergence groups. Smaller changes, such as those encountered at Urbana, suggest that selection for the polymorphic termination of diapause operates at at least a low level in every year. On the other hand, factors other than differential survival may in part account for these variations. Although polymorphic termination has a genetic basis, environmental factors might affect its phenotypic expression. In other words, the proportion of the population which could potentially emerge with Group I might be greater than the proportion which actually does emerge with Group I—the difference varying with environmental influences. This might explain what happened in 1968 when in Chicago almost 50% of a group of locally collected pupae produced Group I moths (A. M. Young, personal communication) while the other half of the same collection, moved to Urbana before winter, produced only 17.6% Group I moths (Fig. 2, Table III). The total mortality in this collection was far from sufficient to account for this difference.

It would be interesting to know how the mean proportions of the two emergence groups vary geographically. There might, for example, be a systematic variation from north to south.

The establishment of a genetic basis for bimodality is in agreement with our earlier suggestion (Sternburg and Waldbauer, 1969) that emergence with Group I or Group II is an expression of an inherent property of the individual. In the earlier paper we arrived at this conclusion by comparing curves obtained in two ways. The first were curves of adult emergence from cocoons collected locally early in the fall and kept during the winter and spring in an insectary under conditions common to all. The second were flight curves obtained by trapping males which emerged from that portion of the local population of pupae which remained in the field in a variety of microenvironments. The fact that the two sets of curves were in phase and included similar proportions of Group I and Group II emergers indicated that bimodality could not be ascribed simply to differences in the microenvironments in which the cocoons spent the winter and spring.

It has been suggested that the emergence groups of *Cecropia* might constitute two sibling species which are morphologically indistinguishable (Ferguson, 1972, page 251). This is obviously impossible. Although the two groups are well separated in time they are clearly not reproductively isolated from each other since the adults of both groups produce a mixed lot of progeny, some of which emerge with Group I and some of which emerge with Group II.

We originally proposed (Sternburg and Waldbauer, 1969) that the bimodal emergence of *Cecropia* is actually the expression of overlapping latitudinal adaptations of the diapause terminating mechanism. This explanation now seems altogether improbable in light of the results given above (Fig. 3, Table III).

There have been many reports of intraspecific geographical adaptations of the diapause-controlling mechanisms of various species, but most of these have been of changes in the critical daylength required for the *induction* of diapause (Danilevskii, 1965; Danilevskii *et al.*, 1970). There are few reports of intraspecific geographical adaptations of the mechanisms which *terminate* diapause. Indeed, Danilevskii *et al.* (1970) offered the generalization that when diapausing stages are moved to the north of the range they resume development in the spring simultaneously with the native population. The implication is, of course, that the environmental prerequisites for the resumption of development are identical for the two groups, and that there has, therefore, been no geographical adaptation.

Cecropia's response is thus unexpectedly complex. When diapausing Group I pupae were moved from Urbana north to Chicago or *vice versa* the adults did emerge more or less synchronously with the native adults. Obviously, Group I exhibits little or no geographic adaptation in diapause termination. Group II pupae, on the other hand, are able to delay the onset of development for a long period of time under conditions which permit Group I pupae to complete their development. Furthermore, the duration of the delay is susceptible to geographic adaptation; as pointed out above, the emergence of Group II follows more quickly after the emergence of Group I in the Chicago population than it does in the Urbana population (Figs. 2, 3, 4, Table IV). It is this difference in the duration of the delay which is largely responsible for the asynchronous emergence of native and transported adults.

As pointed out above, Group I pupae begin to develop in Urbana very early in the spring—at the end of March or the beginning of April. It is likely that in these pupae diapause is terminated simply by chilling, as suggested by Williams (1956), and that adult development begins just as soon as it becomes warm enough. Group II pupae obviously need something more to terminate their diapause. We assume that the latitudinal differences reflect quantitative modifications of the same mechanism which permits Group II pupae to delay the onset of development. We do not believe that qualitatively different mechanisms are involved. It is logically possible that the responsible factor is simply the passage of time. However, it seems more likely that the mechanism requires a response to some environmental factor. This might be a cumulative response or a trigger-like response to a "cue." Photoperiod alone is probably not responsible. If it were, Group II pupae would presumably respond to the lengthening days of spring by initiating development when the photophase becomes sufficiently long. Thus a transfer to the north should result in earlier emergence rather than later emergence as is the case.

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SUMMARY

Hyalophora cecropia (L.) is dimorphic for the termination of diapause at Urbana and Chicago, Illinois, about 40°6' and 41°51' north latitude respectively. Under natural conditions the emergence of the adults is clearly bimodal in both places. At Urbana the early emergers (Group I) initiate development at the end of March and emerge during the second half of May; the late emergers (Group II) initiate development at the beginning of June and emerge during the second half of June and the first week of July. Members of either group produce some progeny which emerge with Group I and a majority which emerge with Group II.

The bimodality has a genetic basis. In either two or three generations we were able to line select from the Urbana population strains which averaged over 75% emergence with Group I as compared with the average of about 8% which was typical of the wild population.

Reciprocal transfers in the fall of wild-collected cocoons between Urbana and the Chicago area revealed that Group II exhibits geographic adaptation but that Group I does not. Pupae transferred in either direction produced Group I adults which emerged more or less synchronously with the local wild Group I. On the other hand, in Chicago the median emergence date of Group II Urbana moths was two weeks *later* than the median emergence date of the local Group II; in Urbana the median emergence date of Group II Chicago moths was twelve to fourteen days *earlier* than the median emergence date of the local Group II.

Rearing the progeny of Chicago moths in Urbana established that there is a genetic basis for the difference in emergence time between the Urbana and Chicago populations. Group II of the Urbana-reared F₁ and F₂ descendants of Chicago *cecropia* continued to emerge earlier than the local Group II. Furthermore, Group II of the F₂ generation emerged synchronously with wild Group II individuals collected in Chicago and transferred to Urbana the previous fall.

Whether a transfer was involved or not, the interval between the emergence of Groups I and II was shorter for the Chicago population than for the Urbana population, the time between median emergence dates averaging nineteen and twenty-eight days, respectively, for the Chicago and Urbana populations.

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Note added in proof: Mr. C. B. Worth (R.D., Delmont, N.J. 08314) (1973, unpublished manuscript) recently informed us that the emergence pattern of *Cecropia* is bimodal in Cape May County, New Jersey and that he has demonstrated that early and late emergence have a genetic basis.

